Spectral properties of excitable systems subject to colored noise

Jannis Schuecker[1], Markus Diesmann[1,2], Moritz Helias[1]

[1] Institute of Neuroscience and Medicine (INM-6) and Institute for Advanced Simulation (IAS-6), Jülich Research Center and JARA, Jülich, Germany
[2] Department of Psychiatry, Psychotherapy and Psychosomatics, Medical Faculty, RWTH Aachen, German

Motivation

- Theory of correlated activity in recurrent networks relies on single neuron response to a modulation of its input, i.e. the transfer function [1]
- Analytical expression for leaky integrate-and-fire (LIF) model only exists for white synaptic noise [2,3]
- For small synaptic time constants only the limit for high frequencies is known [6]
- Stationary case: Colored noise solution obtained by reduction to lower dimensional effective system, respecting the details of the noise in the boundary conditions [4,5]
- **Here: Extension to time dependent case reveals analytical expression for colored noise transfer function [7]**

Neuron and noise models

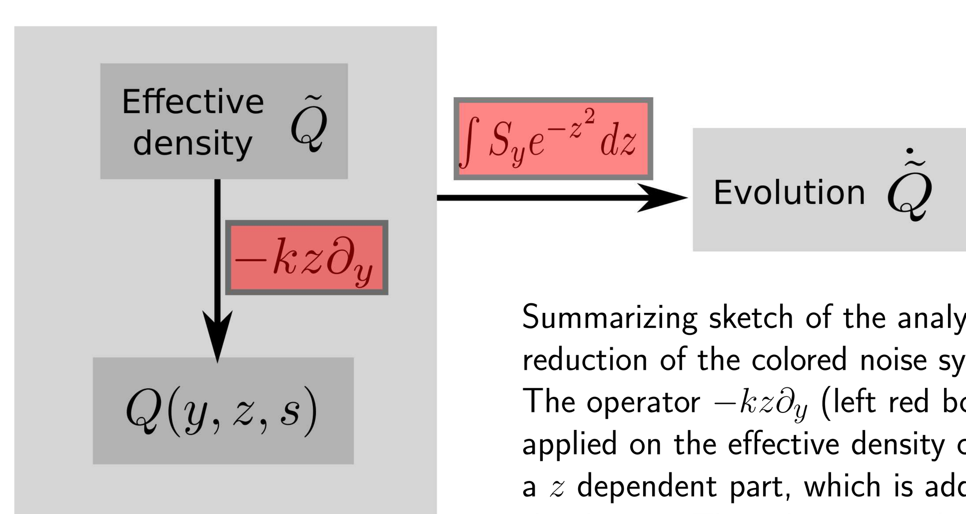
- LIF neuron model with δ-shaped PSC's in diffusion approximation
$$\tau\dot{V} = -V + \mu + \sigma\sqrt{\tau}\eta(t) \qquad (1)$$
with a unit variance **white noise** $\langle \eta(t+s)\eta(t)\rangle = \delta(s)$
- LIF neuron model with exponentially-shaped PSC's in diffusion approximation
$$\tau\dot{V} = -V + I + \mu \qquad (2)$$
$$\tau_s\dot{I} = -I + \sigma\sqrt{\tau}\eta(t), \qquad (3)$$
- Shape of auto-correlation of I characterized by single time scale τ_s
$$\langle I(t)I(t+s)\rangle = \frac{\sigma^2}{2k^2}e^{-|s|/\tau_s}$$
representing **colored noise**, where k relates the two time constants $k=\sqrt{\frac{\tau_s}{\tau}}$
- Assuming small k, V integrates I on a time scale $\tau \gg \tau_s$, so the effective quantity determining the variance of V is the integral of the auto-correlation-function of I over large times
$$\int \frac{\sigma^2}{2k^2}e^{-|s|/\tau_s}ds = \tau\sigma^2.$$
- Consider limit $k\to 0$: $I(t)$ follows $\eta(t)$ instantaneously, so $I(t) = \sigma\sqrt{\tau}\eta(t)$ and the integral of the auto-correlation-function is again
$$\int \tau\sigma^2\delta(s)ds = \tau\sigma^2$$

White noise transfer function

- Dimensionless Fokker-Planck equation for leaky integrate-and-fire neuron model exposed to white noise
$$\partial_s\rho(x,s) = -\partial_x\underbrace{(-x-\partial_x)}_{\equiv S_0}\rho(x,s) \equiv \mathcal{L}_0\,\rho(x,s) \qquad (4)$$
with $x=\frac{\sqrt{2}(V-\mu)}{\sigma}$, $s=t/\tau$ and $\rho(x,s) = \frac{\sigma}{\sqrt{2}}p(V,t)$
- Modulation of neuron's input
$\mu(t) = \mu + \epsilon\mu e^{i\omega t}, \sigma^2(t) = \sigma^2 + H\sigma^2 e^{i\omega t}$
- Linear approximation of the neuron's response
$\nu(t) = \nu(1+n(\omega)e^{i\omega t})$, where $n(\omega)$ is the **transfer function**
- Modulation causes perturbation of the Fokker-Planck equation
$$\partial_s\rho(x,s) = \underbrace{\partial_x(x+\partial_x)}_{\equiv\mathcal{L}_0}\rho(x,s) + e^{i\omega\tau s}\underbrace{\left(-G\,\partial_x + H\partial_x^2\right)}_{\equiv\mathcal{L}_1}\rho(x,s).$$
- Perturbation ansatz $\rho(x,s) = \rho_0(x)+\rho_1(x)\,e^{i\omega\tau s}$ yields differential equation for the time modulated part of the density
$$i\omega\tau\,\rho_1 = \mathcal{L}_0\rho_1 + \mathcal{L}_1\rho_0.$$
- Ansatz $\rho(x,s) = u(x)q(x,s)$ with $u(x) = e^{-\frac{1}{4}x^2}$ yields
$$(i\omega\tau + a^\dagger a)\,q_1 = (G\,a^\dagger + H\,(a^\dagger)^2)\,q_0,$$
with operators $a\equiv\frac{1}{2}x+\partial_x, a^\dagger\equiv\frac{1}{2}x-\partial_x$ and $a^\dagger a$ is Hermitian
- Particular solution constructed from eigenfunctions
$a^\dagger a\,(a^\dagger q_0) = a^\dagger q_0$ and $a^\dagger a\,(\,a^{\dagger 2}q_0) = 2\,a^{\dagger 2}q_0$
$$q_p = \left(\frac{G}{1+i\omega\tau}\,a^\dagger q_0 + \frac{H}{2+i\omega\tau}\,a^{\dagger 2}q_0\right).$$
- First term originating from a variation of μ corresponds to the first excited mode of the system. Second term originating from the modulation of σ corresponds to the second excited mode of the system
- Homogeneous solution as linear combination of parabolic cylinder functions
$$q_1(x) = q_p(x) + \begin{cases} c_{1-}U(z,x) \text{ for } x < x_r \\ c_{1+}U(z,x) + c_{2+}V(z,x) \text{ for } x_r \le x < x_\theta, \end{cases}$$
- Boundary conditions on value and derivative of general solution
$$q_1(x)|_{\{x_r,x_\theta\}} = 0;\quad \tau\nu_0\,n(\omega) = u\,(S_0q_1+S_1q_0)|_{\{x_r,x_\theta\}} \qquad (5)$$
determine four unknows $c_{1-}, c_{1+}, c_{2+}, n(\omega)$
- Transfer function in agreement with [2,3]
$$n(\omega) = \frac{G}{1+i\omega\tau}\frac{\Phi'(z,x)|_{x_\theta}^{x_r}}{\Phi(z,x)|_{x_\theta}^{x_r}} + \frac{H}{2+i\omega\tau}\frac{\Phi''(z,x)|_{x_\theta}^{x_r}}{\Phi(z,x)|_{x_\theta}^{x_r}}, \qquad (6)$$

Effective diffusion

- General time dependent two dimensional system of stochastic differential equations
$$\partial_s y = f(y,s) + \frac{z}{k}$$
$$k\partial_s z = -\frac{z}{k} + \xi,$$
- Two dimensional Fokker-Planck equation for $Q(y,z,s) = \sqrt{\pi}e^{z^2}P(y,z,s)$
$$k^2\partial_s Q = LQ - k^2\partial_y S_y Q$$
with flux operator $S_y = f(y,s) + \frac{z}{k}$ and $L = \frac{1}{2}\partial_z^2 - z\partial_z$
- Goal: Determine first order correction to the marginalized probability flux
$$\nu_y(y,s) \equiv \int dz\,\frac{e^{-z^2}}{\sqrt{\pi}}S_yQ$$
- Perturbative treatment $Q(y,z,s) = \sum_{n=0}^2 k^n\,Q^{(n)}(y,z,s)+O(k^3)$
$$LQ^{(1)} = z\partial_y Q^{(0)} \qquad (7)$$
$$LQ^{(2)} = -\partial_s Q^{(0)} + z\partial_y Q^{(1)} + \partial_y f(y,s)Q^{(0)}.$$
- Collecting all terms which contribute to ν_y in first order and neglecting higher orders
$$Q^{(1)}(y,z,s) = Q_0^{(1)}(y,s) - z\partial_y Q^{(0)}(y,s) \qquad (8)$$
$$Q^{(2)}(y,z,s) = -z\partial_y Q_0^{(1)}(y,s)$$
- First order correction to the marginalized flux
$$\nu_y(y,s) = \left(f(y,s) - \frac{1}{2}\partial_y\right)\tilde{P}(y,s) + O(k^2),$$
where $\tilde{P}(y,s) = \int dz\,\frac{e^{-z^2}}{\sqrt{\pi}}Q(y,z,s) = Q^{(0)}(y,s) + kQ_0^{(1)}(y,s)$
- **Effective Fokker-Planck equation**
$$\partial_s\tilde{P} = -\partial_y\nu_y(y,s)$$
identical to (4) with $y=\sqrt{2}x$ and $f(y,s) = -y$.



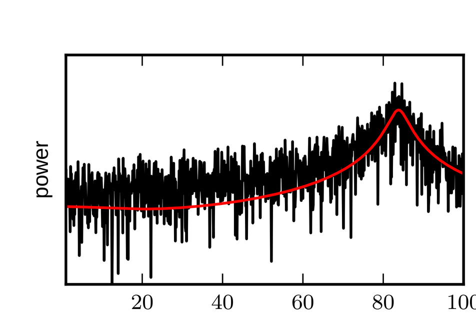
Summarizing sketch of the analytical reduction of the colored noise system: The operator $-kz\partial_y$ (left red box) applied on the effective density creates a z dependent part, which is added to the density. Then the marginalized flux operator $\int S_y dz$ (right red box) is applied to the resulting sum yielding the time derivative of the effective density.

Colored noise

- We obtain an analytical expression for the colored-noise transfer function n_{cn}, replacing $x_{\{R,\theta\}}\to x_{\{\tilde{R},\tilde{\theta}\}}$ in the white-noise solution (6)
$$n_{\mathrm{cn}}(\omega) = n(\omega)|_{H=0} + \sqrt{\frac{\tau_s}{\tau}}\frac{\alpha}{\sqrt{2}}\frac{G}{1+i\omega\tau}\left(\frac{\Phi''_\omega|_{x_\theta}^{x_R}}{\Phi_\omega|_{x_\theta}^{x_R}} - \left(\frac{\Phi'_\omega|_{x_\theta}^{x_R}}{\Phi_\omega|_{x_\theta}^{x_R}}\right)^2\right),$$
- The first correction term is similar to the H-term in (6): colored noise has a similar effect on the transfer function as a modulation of the variance
- The analytical prediction is in agreement with the simulations up to moderate frequencies (Fig.2 A/B)
- Qualitative change compared to whote-noise case (Fig.2 C/D):
  - Synaptic filtering increases the dc-susceptibility counter to the behavior of the decreasing firing rate (Fig.2 C)
  - Synaptic filtering reduces the cutoff frequency (Fig.2 C, inset)
- Qualitative changes are fully explained by a shift in the reset and the threshold (Fig.2 E,F)
- Deviations for higher frequencies expected since in the perturbation (7) we assume $\omega\tau k \ll 1$ only valid up to moderate frequencies
- In the high frequency limit the two correction terms cancel each other

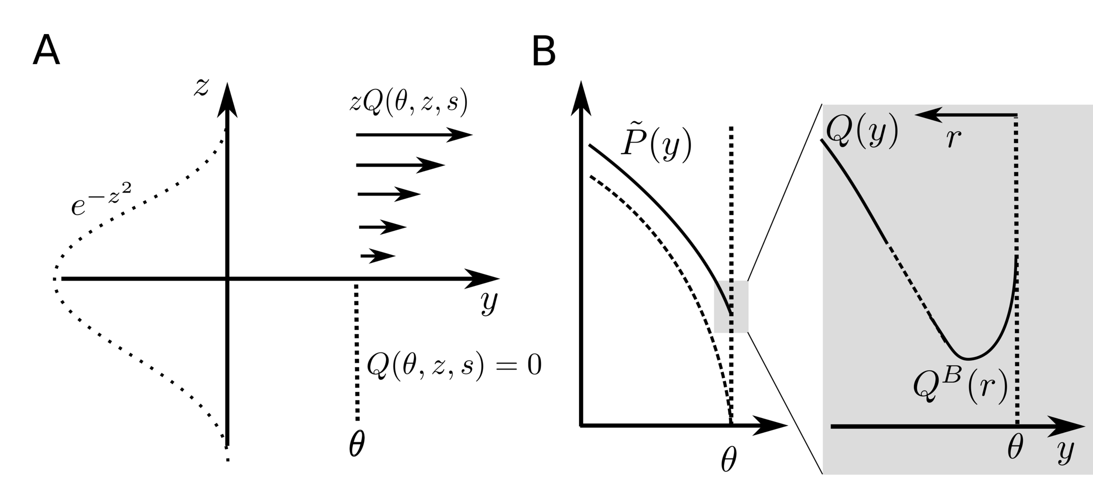
Summary and Outlook

- For a generic first order stochastic differential equations that are driven by fast colored noise, colored-noise approximations for stationary but more importantly also for dynamic quantities are directly obtained by shifting the location of the boundary conditions in the white-noise solutions
- The analytical expression of the transfer function can be used to study:
  - Transmission of correlations by pairs of neurons
  - Study oscillations of population activity in layered networks [8]



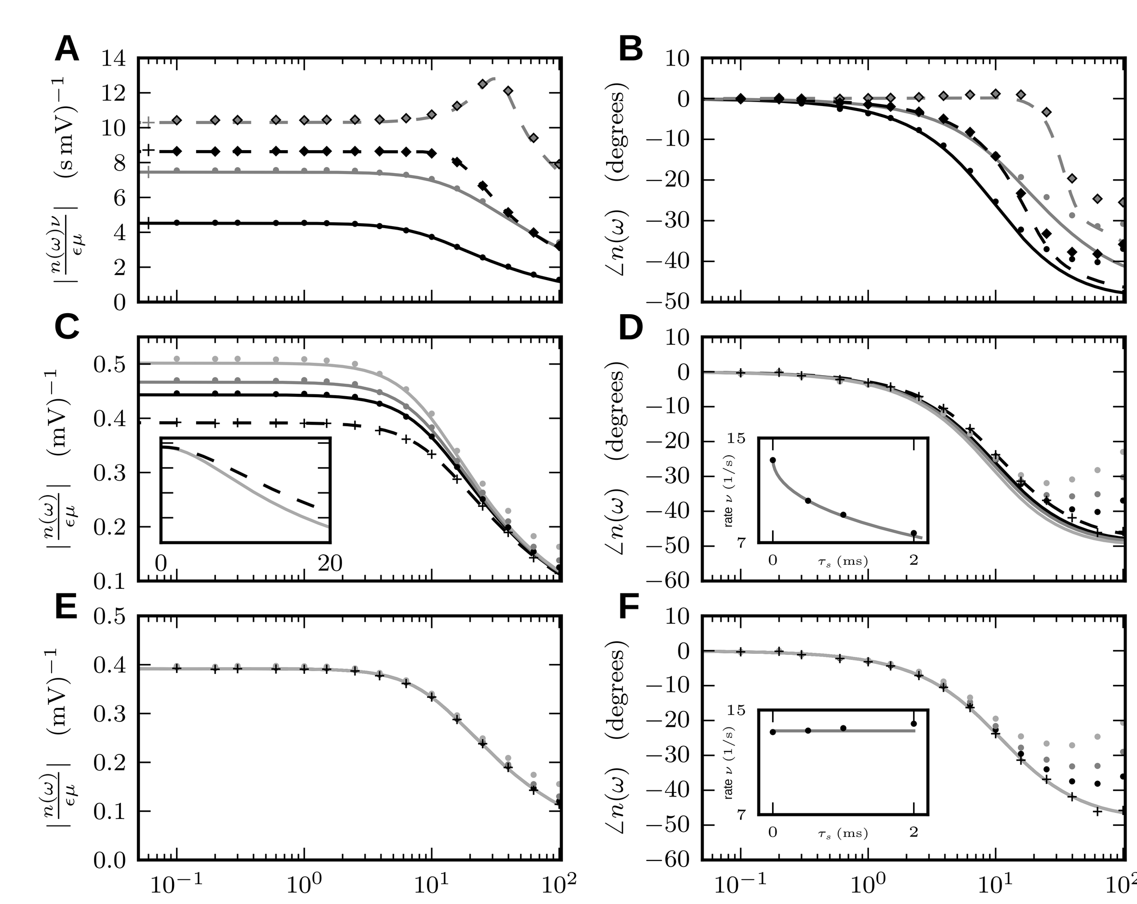
Boundary conditions

- Absorbing boundary at $y=\theta$ and following reset to $y=R$
- Flux must vanish for negative z at threshold
$$0 = \frac{z}{k}Q(\theta,z,s),$$
with $z+kf(\theta,s)\to z$
- Zoom into boundary layer with coordinate $r=\frac{y-\theta}{k}$ with solution
$$Q^B(r,z,s) \equiv Q(y(r),z,s)$$
- Perturbative treatment and half range expansion gives first order boundary layer solution
$$Q^{B(1)}(r,z,s) = \sqrt{2}C(s)\left(\frac{\alpha}{2}+z-r+\frac{1}{\sqrt{2}}\sum_{n=1}^{\infty}\beta_n V_n^-(-\sqrt{2}z)\;e^{\sqrt{2n}r}\right) \qquad (9)$$
- Boundary layer solution must match outer solution. The latter varies only weakly on the length scale of r: First order Taylor expansion of the outer solution at the boundary yields the matching condition
$$Q^B(r,z,s) = Q(\theta,z,s) + kr\,\partial_y Q(\theta,z,s)$$
- Using the general solution (8) gives for the first order
$$Q^{B(1)}(r,z,s) = Q_0^{(1)}(\theta,s) + 2\nu_y^{(0)}(s)\,(z-r) \qquad (10)$$
- Equating (10) to (9) determines $Q_0^{(1)}(\theta,s) = \alpha\nu_y^{(0)}(s)$
- Analogous treatment of reset
- **The effective Fokker-Planck equation has time-dependent boundary conditions determined by the flux of the white-noise system**
$$\tilde{Q}(\theta,s) = \tilde{Q}(y,s)\big|_{R-}^{R+} = k\alpha\nu_y^{(0)}(s) \qquad (11)$$
- **To first order in k this is equivalent to a white noise boundary condition at shifted threshold $\tilde{\theta} = \theta + k\frac{\alpha}{2}$**
$$\tilde{P}(\tilde{\theta},s) = \tilde{P}(\theta,s) + k\frac{\alpha}{2}\partial_y\tilde{P}(\theta,s) + O(k^2) = O(k^2) \qquad (12)$$



A Flux and boundary condition in the two-dimensional colored noise system. On the negative half plane $z<0$ the density must vanish at threshold θ.

B Density of the white noise system (dashed) vanishes at threshold. The density of the effective system has a finite value at threshold which is determined by the matching between the outer solution Q and the boundary layer solution Q^B (right).



Dependence of transfer function of LIF model on synaptic filtering. Absolute value (left column) and phase (right column) of the transfer function for $\theta = 20\,\mathrm{mV}$, $V_r = 15\,\mathrm{mV}$, $\tau_m = 20\,\mathrm{ms}$.
Upper row (A,B): $\tau_s = 0.5\,\mathrm{ms}, \sigma = 4\,\mathrm{mV}$ (solid), $\sigma = 1.5\,\mathrm{mV}$ (dashed), firing rate $\nu = 10\,\mathrm{Hz}$ (black) and $\nu = 30\,\mathrm{Hz}$ (gray). Analytical prediction $\tilde{n}$ (solid curves), direct simulations (dots, diamonds), and zero frequency limit $\frac{d\nu}{d\mu}$ (crosses).
Middle row (C,D): $\sigma = 4\,\mathrm{mV}$, white noise (dashed), colored noise $\tau_s \in [0.5,1,2]\,\mathrm{ms}$ (from black to gray) and $\tau_s = 2\,\mathrm{ms}$ normalized to zero frequency limit of white noise (gray, inset).
Lower row (E,F): same as (C,D) but threshold and reset shifted $\{\theta,R\}\to\{\theta,R\} - \sqrt{\tau_s/\tau}\frac{\alpha}{2}$ to maintain constant firing rate.

References/Acknowledments

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